

CANINE FUNCTION IN *SMILODON* (MAMMALIA; FELIDAE; MACHAIRODONTINAE)

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ABSTRACT. A number of sabertoothed mammal features, exemplified by *Smilodon* from Rancho La Brea, cannot be reconciled with hypotheses that the upper canines were used for stabbing or slashing: the relatively dull sabers which would require enormous force to penetrate the hide of a prey animal, the robust mandible with functional but small canines, the geometric relationships of the skull and the reconstructed head-depressing musculature, and the presence of canine opposition (necessary for biting but not for stabbing or slashing). It is also difficult to envision intermediate steps of behavior and morphology in the multiple evolution of stabbing or slashing from biting ancestors. These apparent anomalies can be resolved (and other features can be explained) by hypothesizing that the upper canines were employed in a shearing, as opposed to puncturing, bite accomplished by depressing the cranium against immobilized mandibles. The probable area of attack was the abdomen. Most, if not all, other sabertoothed mammals appear to possess canine opposition and probably employed some variation of the attack methodology suggested for *Smilodon*. Several lines of evidence suggest that *Smilodon* possessed some degree of cooperative social behavior. The attack methods of the extant Komodo dragon, *Varanus komodoensis*, appear to be analogous to those hypothesized for *Smilodon* and the extinct giant varanids of Australia may have preempted the niche occupied by sabertoothed mammals on other continents.

INTRODUCTION

The suite of unusual specializations which typify sabertoothed mammals has intrigued researchers for decades. Practically every possible mode of saber use has been postulated, including using them as "can-openers" for glyptodonts (Brandes, 1900) or for slicing carrion (Bohlin, 1940). Matthew (1901) refers to earlier suggestions (without citation) that sabertooths used their canines to grub for marine molluscs as walruses supposedly do, as tree climbing aids, or (in forms with reduced mandibular flanges) to stab with the mouth closed.

More recent studies (e.g., Hough, 1949; Miller, 1969; Gonyea, 1976; Martin, 1980; and Emerson and Radinsky, 1980) have firmly established sabertooths as active predators well adapted to catching prey and eating meat. Presently accepted hypotheses concerning saber function usually center about their use in stabbing and/or slashing, probably at the throat

of their prey. While these interpretations appear to be consistent with many sabertooth specializations, other considerations have led me to question the efficacy of this type of attack.

One difficulty I have with accepting a stabbing or slashing attack by *Smilodon* involves the problem of forcing a pair of such weapons into the hide and flesh of a prey animal. As compressed and seemingly sharp as the sabers may be, they are far from being equivalent to a steel knife. Forcing even a slightly dulled steel knife through the hide of a large mammal can be very difficult. Other mammalian carnivores with conical canines use the opposing force of the lower canines to facilitate penetration of the upper canines (and vice versa) during an attack. If they simply tried to force the upper canines into their prey without using the lower canines, they would fail. Similarly, if *Smilodon* were to try to stab or slash without an opposing force, considerable momentum would have to be built up by the time the sabers contacted the prey. I believe that the problem of developing enough force to drive a pair of rather dull sabers into hide and flesh raises serious questions about any stabbing or slashing hypothesis.

An important theoretical point involves the fact that sabertooth adaptations arose independently within at least four different groups of mammals—borhyaenid marsupials, creodonts, nimravids, and felids. As the normal kill method in all living mammalian carnivores (and, presumably, all ancestors of sabertoothed types) is the canine bite, postulating a slash or stab requires the multiple, convergent development of a radically different method of kill behavior. I find it impossible to envision the necessary intermediate combinations of morphology and behavior that would be required by a gradualistic model of evaluation and equally impossible to accept that such a complex combination of changes could occur even once within the framework of punctuated models.

These and other difficulties with the slashing/stabbing hy-

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potheses raised the question of whether the peculiar specializations of sabertoothed mammals have resulted in more radical interpretations of saber function than is necessary. In an effort to address this question, I studied the large Rancho La Brea sample of *Smilodon* in the collections of the George C. Page Museum (specimen prefixes LACMHC and LACMRLP), a branch of the Natural History Museum of Los Angeles County (LACM).

MORPHOLOGY

Three character complexes were most important in the development of the various slashing/stabbing hypotheses: (1) the apparently weak mandible with a reduced canine which does not appear to have been of much use during an attack, (2) the evidence for powerful head-depressing muscles which could be used in a stabbing or slashing action, and (3) the striking hypertrophy of the upper canines which immediately conjures up images of the edged weapons man uses to slash or stab. Re-examination of these characters and consideration of other morphologic features yield additional information not always in agreement with previous interpretations.

OVERALL STRUCTURE

The *Smilodon* from Rancho La Brea approximated the size of a modern African lion but had very powerful forelimbs, a proportionately larger head, and a short tail. The forelimbs, with their large, retractile claws (Gonyea, 1976), would have been very well suited to pulling down and immobilizing fairly sizable prey animals. Limb and foot structure and proportions (Merriam and Stock, 1932; Gonyea, 1976; Martin, 1980; Shaw and Tejada-Flores, in press) and vertebral structure (Merriam and Stock, 1932; Slijper, 1946) indicate that *Smilodon* was not cursorial but probably was capable of short, rushing attacks. Most recent authors generally agree that *Smilodon* probably stalked close to its potential prey, then rushed a short distance from ambush. I believe that the massive forelimbs were employed in grasping the upper part of the prey's body from the side and pulling it down towards the attacker so that the abdomen would be exposed on the opposite side. This method of bringing down prey is similar to that often used by many of the larger living felids when

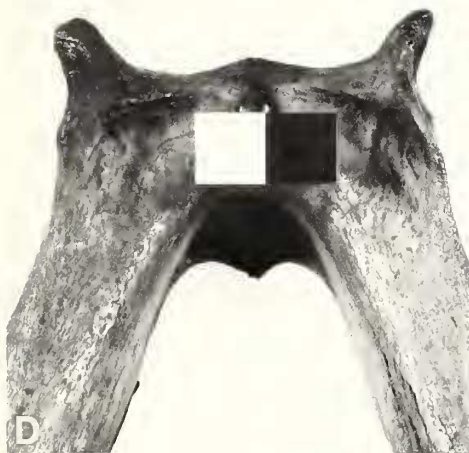
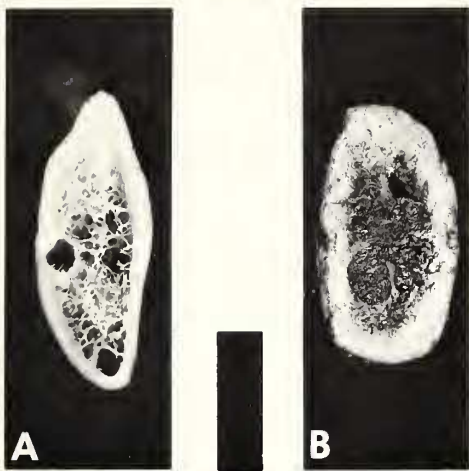
attacking large prey except that they may also employ their teeth in the attack (Leyhausen, 1979; Schaller, 1967, 1972).

MANDIBULAR COMPLEX

The greatly reduced coronoid process has been repeatedly used as evidence for a relatively weak bite (e.g., Matthew, 1910; Merriam and Stock, 1932) because it would have provided less leverage for the temporalis muscle. Emerson and Radinsky (1980), elaborating on the work of Kurtén (1952), showed that the probable bite strength during carnassial occlusion was roughly equivalent to that of comparably sized living felids, but at full gape, it was undoubtedly rather weak. This resulted not only from the poor lever arm for the temporalis but also from the reduction of the masseter. They also determined that the relative cross-sectional area of the mandible below the carnassial was about equivalent in sabertooths and living felids. The diastemal region superficially appears weaker in *Smilodon* because it is relatively shallow. However, Figures 1A, B compare cross sections cut through the shallowest part of the diastema in a young adult African lion (*Panthera leo*) and a young adult *Smilodon* of about the same size. Not only is the relatively greater breadth of this area in *Smilodon* readily apparent, but the outer layer of compact bone is far thicker. If anything, the mandible of *Smilodon* appears much stronger than that of the lion. Several longitudinally sectioned and many broken mandibles in the Rancho La Brea collections at the George C. Page Museum demonstrate that this very strong internal construction characterizes the entire *Smilodon* mandible. In overall appearance, the *Smilodon* mandible is stouter than that of the lion with a massive, very rugose symphyseal region (Fig. 1C) most similar to that of *Panthera* among the type III symphyses described by Scapino (1981). The major differences between the two appear in the outline of the symphyses and the distribution of the largest rugosities. In *Smilodon* these occur toward the ventral portion at or near the ventral tubercle while in *Panthera* they are found near the posterior margin. The evidence strongly indicates that powerful forces impinge upon the mandible and that it was not simply used for shearing at the carnassials or pulling flesh off prey in conjunction with the incisors, the only other postulated uses for the mandibular dentition (Emerson and Radinsky, 1980; Miller, 1969).

Forces acting on the mandible have major components transmitted through the condyloid process to the glenoid

Figure 1. *Panthera leo*. A. Cross section through diastema of mandible, LACMRLB JGT2. Rest are *Smilodon*. B. Cross section through diastema of mandible, LACMHC 7108. C. Stereopair of left mandibular symphysis, LACMRLP R11258. D. Ventral view of anterior mandible, LACMHC 2001-2, showing anterior projection of flanges. E. Stereopair of right mastoid process, LACMHC 2001-2 (retroarticular process at bottom). F, G, H. Posteroventral views of left portion of cranium, LACMRLP 20273, and associated atlas, LACMRLP 20276, depicting relationships of atlas and mastoid process. F. Cranium only. H. Cranium with atlas articulated and rotated to extreme anteroventrad position. G. Same as H but with "ghost image" of ammonium chloride coated atlas in double exposure. Note the alignment of portions of the lateral margins of atlas wing and mastoid process between white marks in G. Scales: A, B, F, G, H, scale bar = 2 cm (bar between A and B applies to both and bar on H also applies to F and G). C, D, E in cm.



fossa of the squamosal. This region independently reflects the gross magnitude of such forces. In comparison to the African lion, the neck of *Smilodon*'s condyloid process is much stouter and the condyle is wider with a considerably larger articular surface. In the cranium of *Smilodon*, the retroarticular process is thick and stout, the entire zygoma is very well developed and the base of the zygomatic process of the temporal provides massive support for the glenoid fossa. The entire articular complex and supporting structures demonstrate again that the mandible of *Smilodon* was subjected to very strong forces during some portion of its use.

While the lower canines of *Smilodon* are relatively small in comparison to body size, they are far from vestigial. They approximate the size of canine found in a medium-sized mountain lion (*Felis concolor*) but they appear even smaller because of their proximity to the very large incisors. The lower canines are stout, sharp, and recurved posteriorly with strong roots and relatively thick enamel. Their posterior and medial margins bear sharp, finely serrate ridges (see Merriam and Stock, 1932: pl. 13, figs. 8, 8a). While the medial serrate ridge may have functioned with the incisor battery in worrying loose chunks of meat as described by Miller (1969), the only apparent function for the posterior serrate ridge would have been to facilitate puncturing. Thus, the reduced lower canines of *Smilodon* were still capable of functioning like those of living felids in penetrating the hide and flesh of prey animals, but would not have produced as large or deep wounds as the lower canines of an equivalent-sized true cat. The large roots and the heavy bone surrounding them are evidence that the canines were also subjected to considerable stress.

One often discussed feature of the mandible is the anteroventral mandibular flange. The ventral development of this flange in *Smilodon* is relatively slight, when compared to many other sabertoothed mammals, and quite variable. It has been suggested that a highly developed ventral flange served to protect the sabers from breakage or to protect the neck from accidental injury by the sabers (Scott and Jepsen, 1936; Martin, 1980). A more plausible explanation has recently been advanced by Dawn A. Adams and Daniel B. Adams (pers. comm., 1983), which relates the ventrad development of the flange to a powerful digastric musculature required by forms with nearly vertical occiputs. Several studies (e.g., Schultz et al., 1970) have suggested that the flange became reduced in *Smilodon* to allow stabbing with the mouth closed. This appears to be improbable because there would then be no function for that portion of the posterior serrations on the upper canine which extend dorsad to the ventral border of the closed mandible all the way to the gum line. Furthermore, if the sabers were used to stab with the mouth closed, the proximal serrations should wear smooth more slowly than the distal serrations. None of the La Brea specimens display such differential wear. Also, a major potential problem would result from the shock transmitted to occluding upper and lower teeth (particularly the interlocking incisors) when the mandible struck the prey in a closed mouth stab.

In contrast to the moderate and variable ventral devel-

opment of the flanges, they are consistently well developed anteriorly. The anterior portions of the flanges flare laterally and become slightly thickened at their margins. In ventral view, the anterior outline of the symphyseal region is strongly concave with the symphysis situated at the axis of a considerable depression (Fig. 1D). As described below, I believe that the anterior development of the flange played an important part during *Smilodon*'s attack.

INCISOR BATTERY

The basic form and function of the upper and lower incisors have been well described by Merriam and Stock (1932) and Miller (1969). Overall, they are very large, sharp, recurved posteriorly, and bear huge roots. The bone anterior and posterior to the alveoli is very stout. The incisor battery appears very prognathous with the sharp apices of the upper and lower incisors (and the lower canines) completely interlocking when the jaw is closed (Fig. 2). All tend to bear ridges on their medial and lateral margins. These ridges are usually very finely serrate in unworn teeth with the serrations becoming progressively better developed from the medial (where they may be absent) to the lateral incisors. The ridges curve posteriad toward the bases of the crowns to form cingula which frequently bear small cusps. Placement of the cingular cusps is such that they provide additional shear against the tips of the opposing incisors when the jaw is completely closed. If the incisors were used to gnaw flesh from bones as suggested by Miller (1969), one would expect to find wear on the anterodistal portions of the crowns. None of the examined specimens exhibited such wear. As noted by Merriam and Stock (1932) and further elaborated by Miller (1969), the incisor battery, including the lower canines, forms an immensely powerful puncturing and gripping device. I would add that it was also capable of developing considerable shear between opposing teeth.

HEAD-DEPRESSING MUSCULATURE

A number of osteological characters indicative of powerful head-depressing muscles in various sabertoothed mammals have been cited as evidence supporting a stabbing or slashing attack (Matthew, 1910; Merriam and Stock, 1932). Emerson and Radinsky (1980) question these interpretations, noting that the insertion scars for the rectus capitus ventralis and longus capitus (at the basioccipital-basisphenoid suture) are not unusually well developed and asserting that "the sternomastoid and the eleidomastoid do not leave discrete scars on the mastoid process." While it is true that the insertion scars for the rectus capitus ventralis and the longus capitus are only modestly developed in *Smilodon*, the broad tip of the mastoid process is very rugose with several deep pits (Fig. 1E) which may coalesce to form a large groove. I agree with Merriam and Stock (1932:33) that this area probably served as the insertion for well-developed sternomastoid and cleidomastoid muscles. In addition, the manubrium of the sternum (origin of the sternomastoid) is relatively robust in *Smilodon*. The enlarged mastoid processes would give these muscles considerably more leverage to depress the head than

in typical felines. Another possible explanation for at least a portion of the apparent muscle scars at the tip of the mastoid process is that they served as the area of origin for a very well developed digastric musculature (Dawn A. Adams and Daniel B. Adams, pers. comm., 1983).

There is evidence for additional, and even more powerful, head-depressing muscles in *Smilodon*. The entire posterolateral portions of the enlarged mastoid processes appear to be covered with very large muscle scars (Fig. 1E). Matthew (1910) believed that this area provided attachment for the sternomastoid which had shifted from its normal attachment area at the tip of the mastoid process. However, if the atlas of *Smilodon* is rotated anteroventrally about the atlantooccipital articulation, the parts of the lateral margins of its wings not only align quite well with posterolateral muscle scars of the mastoid processes but would also effectively block other muscles of posterior origin which might potentially insert on these scars (Figs. 1F, G, H). Modern felids and canids possess tiny mastoid processes with only very minute muscles extending between them and the atlas wings. Descriptions of modern felid and canid anatomy often ignore, or are not consistent in the terminology and interpretations of, these muscles. Though quite different in detail, the highly developed mastoid processes of the giant panda, *Ailuropoda*, more closely approximate those of *Smilodon* and their anatomical relationships have been thoroughly described by Davis (1964). He states that the rectus capitus lateralis inserts on the "posterior surface of the mastoid process near its outer edge" (p. 170). The obliquus capitus anterior is described as inserting "just above the mastoid process" (p. 170) but on his figure 20, its insertion is shown as including much of the posterior surface of the mastoid process. Both muscles originate on the ventral surface of the tip of the atlas wing which, in *Smilodon*, is posteriorly elongated and deflected ventrad (Figs. 3A, B; 5A). Thus, it appears highly probable that very well developed muscles (which may or may not be homologous with those of *Ailuropoda*) extended from the ventral surfaces of the atlas wings to the posterolateral margins of the mastoid processes. The enlargement of the atlas wings and mastoid processes in *Smilodon* would give this atlantomastoid musculature increased length and considerable leverage to depress the head about the atlantooccipital articulation. I consider them to have been more important in this action than other head-depressing muscles. Additional evidence for the presence of powerful muscles originating from the ventral portion of the atlas wings is provided by the large attachment area on the axis for the obliquus capitus posterior, which originates from the entire neural arch and inserts on the dorsal surface of the atlas wings (Davis, 1964). This muscle functions to rotate the atlantoaxial articulation and prevents the atlas wings from being drawn anterior during contraction of the atlantomastoid musculature. In comparison to *Panthera*, the neural arch of the axis in *Smilodon* (Fig. 3C) is proportionately larger and extends more posteriad relative to the centrum indicating a well-developed obliquus capitus posterior. Reconstructions of the major head-depressing muscles are depicted in Figure 5A. Overall ventrad movement of the head and neck would have been aided by a

powerful scalene musculature indicated by the enlarged transverse processes on the cervical vertebrae (Matthew, 1910).

All available evidence leads to the almost inescapable conclusion that *Smilodon* possessed strongly developed muscles for head depression, especially those which rotate the atlantooccipital articulation. While these have been used as powerful evidence for a stabbing or slashing mode of saber use, it is not impossible that powerful head depression could have served some other purpose, as will be proposed below.

UPPER CANINES

The saber morphology of *Smilodon* has been well described by Merriam and Stock (1932). To review briefly, they are long, slender, recurved, blade-like teeth with an extremely thin veneer of enamel (Fig. 4). The enamel extends to the gum line along the posterior margin but its extent is variable on the rest of the tooth, averaging only about two thirds as far. Very fine enamel serrations extend from the tip to the gum line on the posterior margin and, variably, between one half to two thirds as far from the tip on the anterior margin. The posterior margin is more compressed than the anterior, especially toward the base of the exposed portion. Here, the anterior margin becomes quite rounded proximal to the termination of the anterior serrations. The serrations are frequently worn, even smooth, in older individuals. Although this wear indicates that the canines were not used simply for display, I believe that the fineness of the serrations and the very thin enamel layer covering the saber in *Smilodon* demonstrate relatively infrequent use (such as during the kill but not regularly during feeding). More frequent use, resulting in more severe wear, should have required thicker enamel and strongly developed serrations. The large root of the upper canine, about 40% of its total length, undoubtedly reflects the need for support during strenuous use.

The bone surrounding the canine alveolus is relatively thin along the medial surface, but this area is braced to some extent by the palatal portions of the maxillary and premaxillary bones. On the lateral surface, it is thin at the alveolar margin but thickens a little toward the root region, especially adjacent to the long axis of the alveolus. Heavier bone occurs along the anterior and posterior margins of the alveolus, indicating more anterior and posterior stress on the canine. In individuals with fully developed canines, very thick bone surrounds the pointed tip of the canine root and extends from the tip along the anterior margin for a short distance. The canine root does not extend as far posteriad as the convex surface on the external portion of the maxillary suggests, but terminates above or slightly anterior to the infraorbital foramen. Younger specimens, in which the canine root is still forming, have alveoli with broadly U-shaped terminations surrounded by relatively thin bone. These canine alveoli also extend farther posteriad, almost to the posterior margin of the maxillary bone. Thus, thickening of the bone is accomplished by a filling in of the alveolus as the root becomes fully formed. The mass of bone at the tip and along the proximal anterior edge of the root is consistent with the need

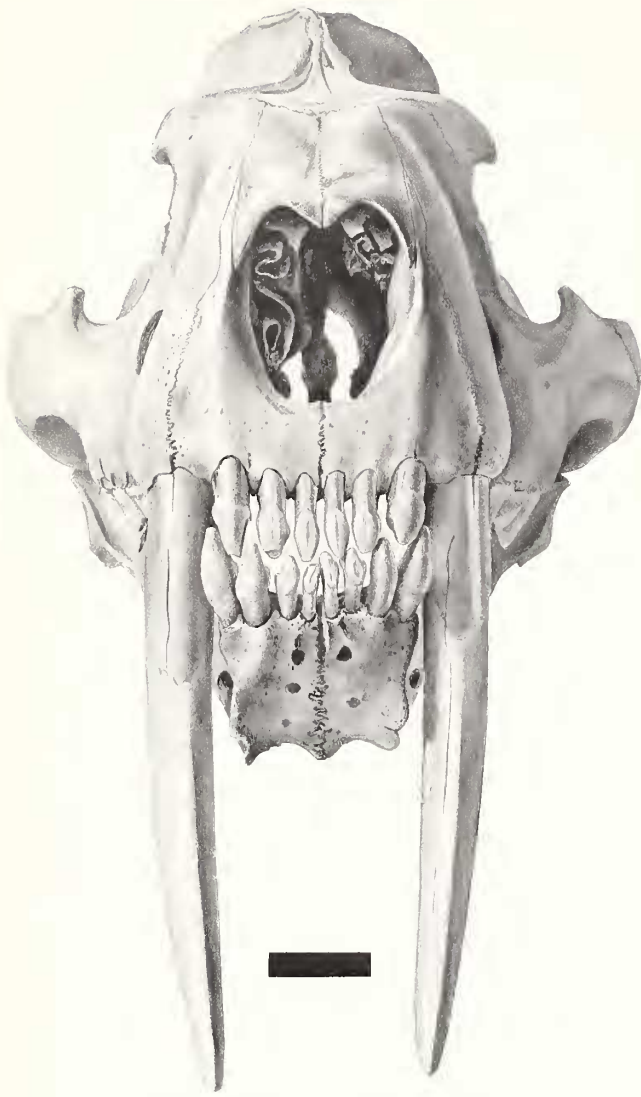


Figure 2. Anterior view of *Smilodon* skull and mandible, LACMHC 2001-1, showing interlocking of incisors. Scale bar = 3 cm. From Merriam and Stock (1932: pl. 2, fig. 3) with permission, Carnegie Institution of Washington.

to provide support for fairly strong forces developed by pushing the tip against a resistant object. If the sabers were used regularly in anterior or posterior slicing actions, I would expect to find more bone supporting the distal portions of the anterior and posterior alveolar margins.

The importance of the sabers to *Smilodon* is illustrated by the similar morphology of the deciduous upper canines which are, however, concave on their medial surfaces in order to accommodate considerable eruption of the permanent canines before the deciduous canines are lost (Merriam and Stock, 1932). Unlike modern felines, in which there is a brief period of time when the deciduous canines have become too weak to use and the permanent canines have not yet erupted

to the point of becoming functional (Leyhausen, 1979), *Smilodon* always maintained functional upper canines (Tejada-Flores and Shaw, 1984).

As briefly, mentioned in the introduction, the supposed knife-like appearance of the sabers is only valid when compared to a typical conical carnivore canine, not when compared to a genuine steel knife. Cross sections through a typical saber (Fig. 4) more nearly resemble somewhat flattened ovals than sections through a metal blade. The very tips of the upper canines, which would initiate penetration of a prey animal's hide and flesh, are rounded both transversely and anteroposteriorly (Figs. 5B, C). Comparison with the upper canines of *Panthera leo* shows that the saber tips of *Smilodon* are little, if any, sharper. The force required to drive one, let alone two, of these formidable looking weapons into a large prey animal would be enormous.

PALATE

The palate of *Smilodon* (Fig. 5D) exhibits a pattern of longitudinal ridges and grooves (Merriam and Stock, 1932:35–36). A highly variable medial ridge usually occurs from the premaxillary-maxillary suture to the posterior margin of the palatines. In some individuals, this ridge may extend more anteriorly while in others, parts or all of it may be very reduced or absent. A lateral ridge occurs on each side of the medial ridge. These are more consistently developed and extend posterolaterad from the anterior margins of the anterior palatine foramina to terminate between the middle and posterior of the palatines. The anterior portions of the lateral ridges bear sharp crests which frequently flare laterally. Posterior to the palatine-maxillary suture, the lateral ridges become subdued and broadened before merging with the palatine surface. A prominent broad groove with a roughened bottom exists between each lateral ridge and the adjacent alveolar margin of the palate. Merriam and Stock (1932:36) suggested that these grooves served as conduits to ingest sucked blood. This appears to be improbable in that the posterior portions of the grooves trend laterally and terminate just medial to the M's, not at mid-palate. In addition, it would be very difficult to seal off the front of the mouth for effective sucking unless the pool of blood was quite deep (Bohlin, 1940).

If the mandible is articulated with the cranium in a closed position (Fig. 5E), however, the rather sharp diastemal crests align exactly with the middle of the palatal grooves with about 4 cm of clearance. This alignment of the palatal ridges and grooves and the diastemal crests of the mandible could serve as a very effective gripping device for thick pieces of flesh held in the anterior of the mouth. Galapagos finches have similar longitudinal ridges and grooves in the horny palate which line up with the margins of the mandibular tomia in order to grip and crush seeds (Bowman, 1961). Use of the palate for gripping would require a much stronger palatal construction than exists in cats with conical canines. In fact, the palate of *Smilodon* is far sturdier than in modern felids of similar size; the bone is thicker, the corrugations

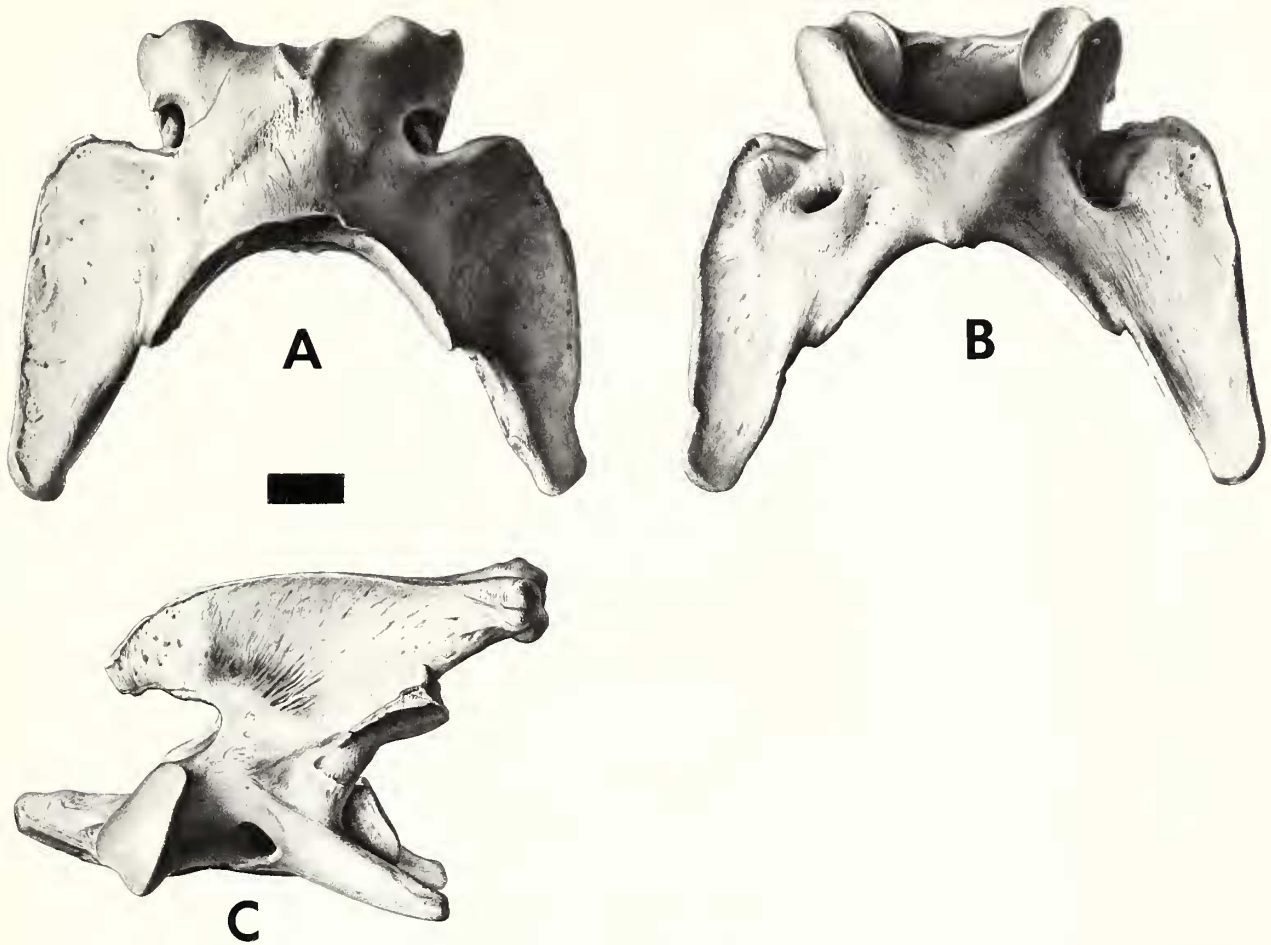


Figure 3. *Smilodon*. Atlas, LACMHC 2038-5: A. Dorsal view. B. Ventral view. Axis, LACMHC 2039-1: C. Lateral view. Scale bar = 2 cm. All from Merriam and Stock (1932: pl. 17, figs. 4, 7, 3) with permission, Carnegie Institution of Washington.

would also serve to reinforce this area, and the palate is partially braced along the midline by the vomer.

CRANIUM-MANDIBLE GEOMETRY

The most important task in determining mode of saber usage is the investigation of types of motion permitted or excluded by the geometric relationships of cranium and upper dentition to mandible and lower dentition. The extent of the gape in *Smilodon* has often been discussed. I agree with Emerson and Radinsky (1980) that the maximum possible gape was about 90 to 95 degrees. As they further point out, this maximum gape results in about the same amount of absolute clearance between the upper and lower canines as does the maximum gape in modern felids of similar size.

In a detailed study of possible modes of saber use by *Smilodon*, Simpson (1941) concluded that the momentum needed for a stabbing attack could be generated by an initial leap. As the sabertooth struck its prey, body momentum would be transferred to the skull which would whip ventrad to drive the sabers home. Simpson omitted the mandible from his

figures and calculations, however, stating that inclusion of the mandible would not have altered his conclusions. If the mandible is added to all of his diagrams and the outline of the prey animal's body is extended in a rounded curve, it is obvious that the mandible, even at maximum possible gape, would strike the prey well before or at least simultaneously with the upper canines. This would either abruptly close the mouth or prevent canine penetration. Bohlin (1947) also showed that when the amount of posterodorsad cranial flexion necessary to generate momentum for a stab is considered, the head would be drawn so far back that the attacker could not have seen its prey, much less the intended area of attack (see his fig. 1). Kurtén (1952) suggested that sabertooths pressed the mouth at full gape against the body of their prey then nodded the head ventrad to stab. While this removes potential problems which would be created by impact of the mandible or inability to see the intended prey, there would now be far too little force for the sabers to penetrate.

Initial penetration of a tapered, sharp blade is best facilitated by motion in the direction of its long axis. Any deviation from the axial direction when the target is struck will

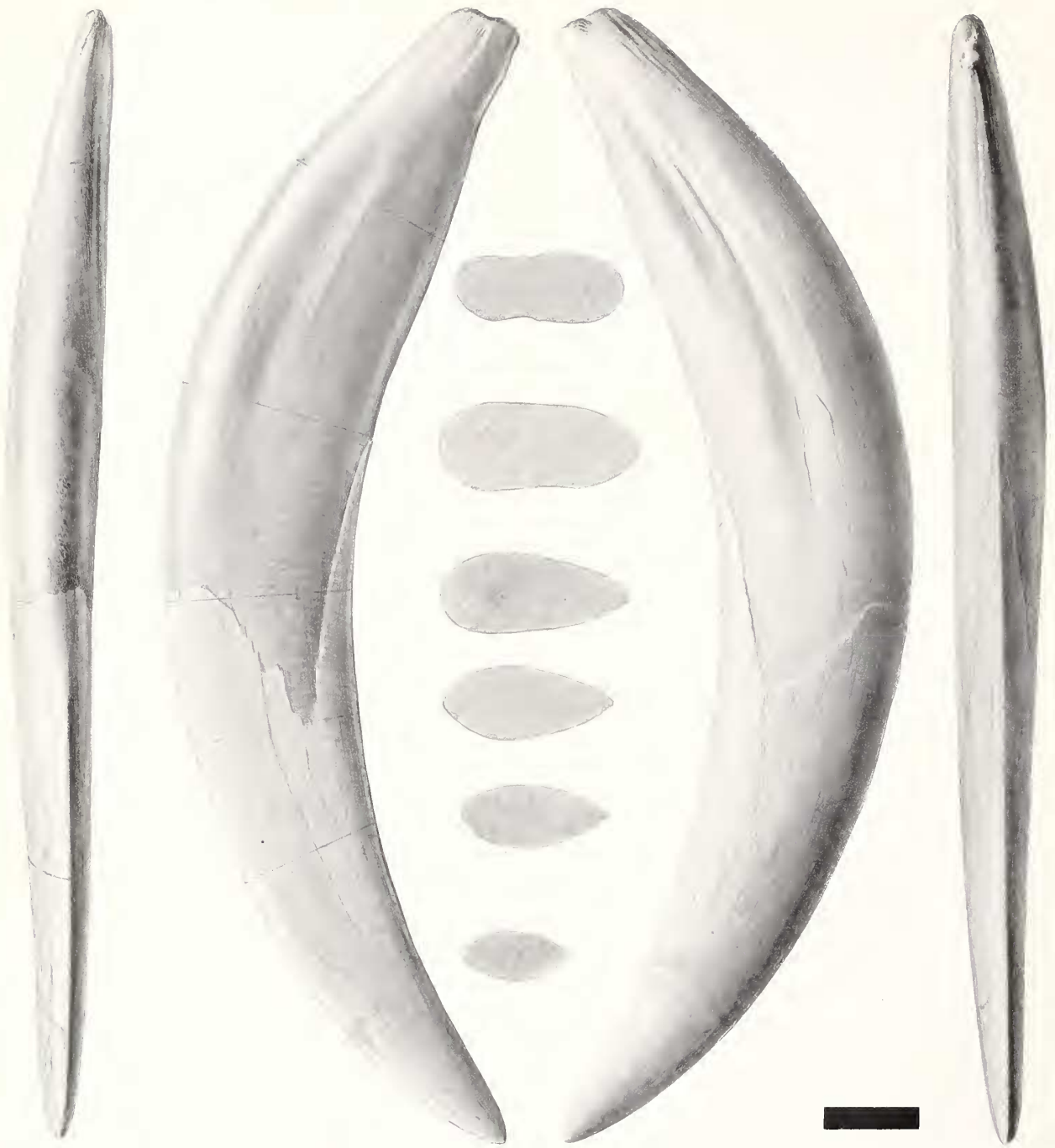
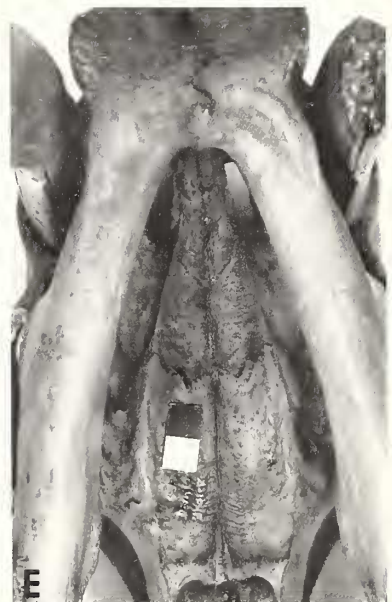
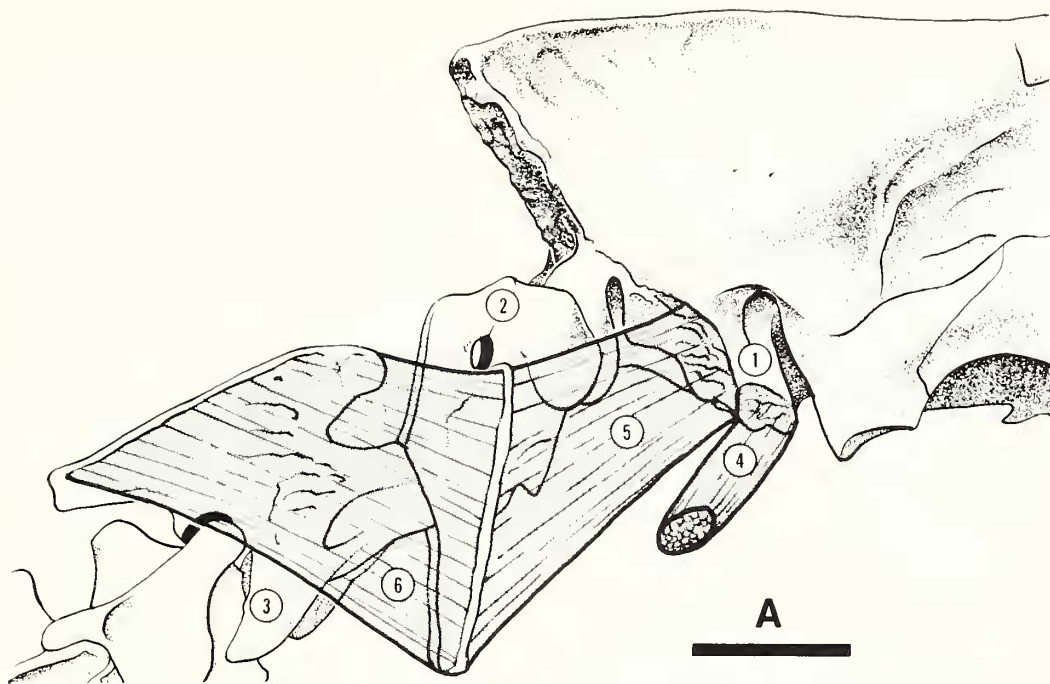


Figure 4. *Smilodon* right upper canine, LACMHC 2000-R.9. From left to right: anterior, medial, cross-sectional, lateral, and posterior views. Scale bar = 2 cm. From Merriam and Stock (1932: pl. 12, fig. 1) with permission, Carnegie Institution of Washington.

Figure 5. *Smilodon*. A. Reconstruction of major head-depressing muscles (1 = mastoid process, 2 = atlas, 3 = axis, 4 = sternomastoid/cleidomastoid, 5 = atlantomastoid musculature, 6 = obliquus capitus posterior) drawn by Mark Hallett. B, C. Lateral and posterior stereopairs of right upper canine tip, LACMHC 2000-R.31. D. Stereopair of palate, LACMHC 2001-2. E. Palatal view of LACMHC 2001-2 with articulated mandible. Scales: A, bar = 5 cm. B, in mm. C, same as B. D, E, in cm.



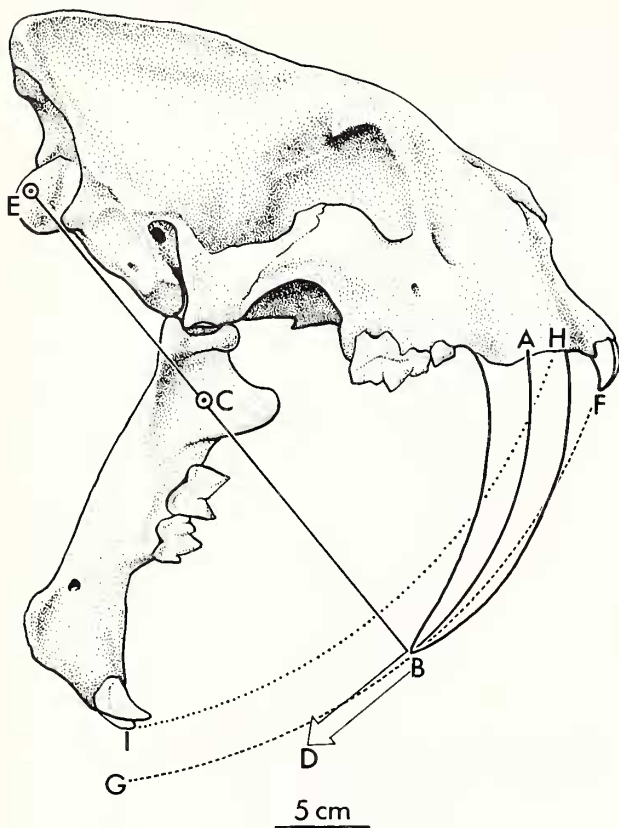


Figure 6. Geometric relationships of *Smilodon* cranium and mandible based on LACMHC 2001-2. See text for explanation. Drawn by Mark Hallett.

result in a larger area of contact and require more initial force to begin a puncture. As noted by Simpson (1941), angulation of the saber axis during a stabbing motion by *Smilodon* would also place a potentially dangerous strain on the saber and its alveolus. Figure 6 illustrates the long axis of the saber and other geometric relationships of the skull and mandibles in *Smilodon*. Arc A-B represents the axis of the upper canine, essentially a perfect segment of a circle with its center at C. The line B-D is tangent to A-B at B and indicates the direction that the tip of the saber must be moving at the moment it contacts a prey animal if it is to achieve the most efficient initial penetration. Clockwise rotation about any point along the radian C-B or its posterodorsal extension will result in the required instantaneous force along the direction B-D. The posterodorsal extension of C-B extends through E, the center of rotation for the atlantooccipital articulation. Thus, the powerful atlantomastoid musculature will rotate the head in precisely the proper motion for most

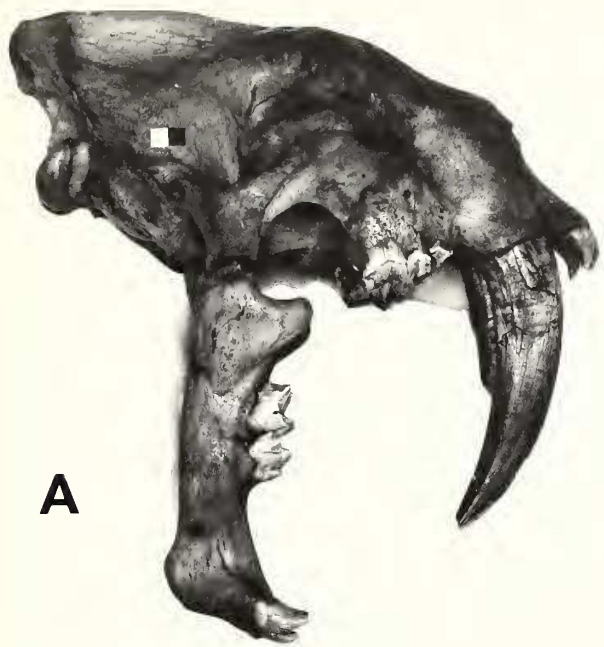
efficient initial penetration of the upper canines. While this configuration may appear to confirm a stabbing mode of attack, further geometric considerations show stabbing to be very improbable, if not impossible. Rotation about point E would result in the tip of the saber moving through the arc F-B-G and the tip of the lower incisors, through the arc H-I. Obviously, the body of a prey animal would have to extend inside of arc F-B-G to be struck at all by the tip of the saber but, if the prey's body extended inside the arc H-I, the lower incisors or mandible would impact before the sabers. As the distance between these arcs is less than 3 cm, a very precise motion would be required to stab or slash without abruptly closing the mouth. Even if this could be accomplished, the curvature of a large prey animal's body would result in the axis of the saber being very oblique to its target and only a glancing blow could be delivered.

If the action of the other head- and neck-depressing muscles were included in a stabbing or slashing action, the center of the resulting complex motion probably could not be represented by a single point. The general area about which movement would center would, however, be farther posteriad and ventrad. This would result in a slightly greater clearance between the paths described by the motions of the tip of the saber and the anterior end of the mandible. It would also result in the long axis of the sabers being at an angle to the direction of force with concomitant loss of efficiency during initial penetration. In the most extreme case of a vertical stab (Simpson, 1941: fig. 1A), only about 12 cm of clearance could be generated. This would still not be enough for a reasonably safe attack using a stabbing or slashing action.

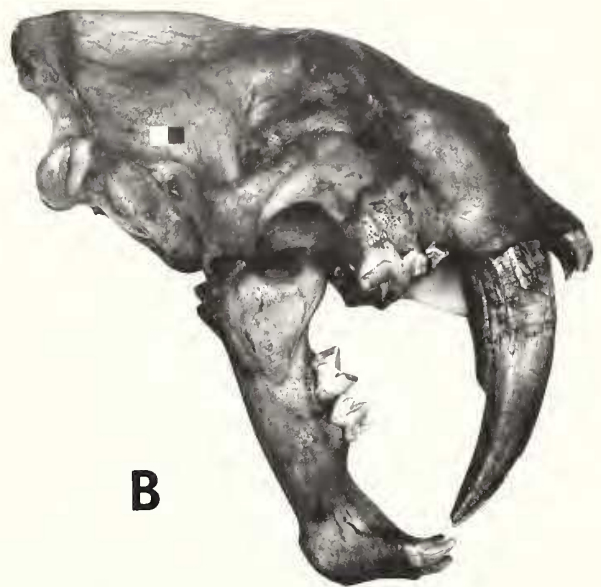
The Rancho La Brea collections of the LACM include at least 600 fairly complete crania of *Smilodon* but their sabers are not as well preserved as the rest of the specimens. The sabers are usually broken off, shattered, or have slipped out of the alveoli. In addition, very few crania have associated lower jaws. As a result, only one cranium with associated mandible (LACMHC 2001-2) contains an almost complete saber in original position and can be used to determine accurately the relationships of the upper and lower canines during closure of the mouth. Manipulation of the specimen immediately demonstrates that, as the tips of the canines pass each other, the tip of the lower passes just interior and anterior to the tip of the upper (Fig. 7B)—exactly the same mode of canine opposition which allows other mammalian carnivores to bite with their canines.

The questions of canine opposition and whether or not sabertoothed mammals could bite with their canines have been addressed by several earlier workers. Pomel (1843) interpreted wear facets on the lateral surfaces of lower canines in *Felis meganthereon* as indicative of canine opposition in that form. In discussing several Old World taxa of saber-

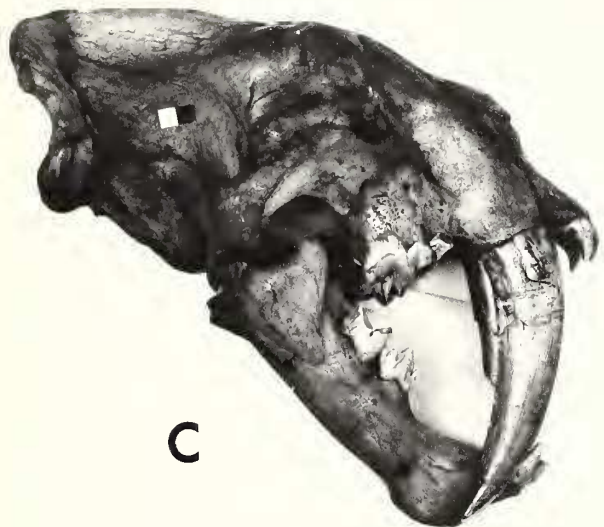
Figure 7. Associated *Smilodon* cranium and mandible, LACMHC 2001-2, depicting mouth closing sequence. A. At maximum gape. See text for explanation of others. Scales in cm.



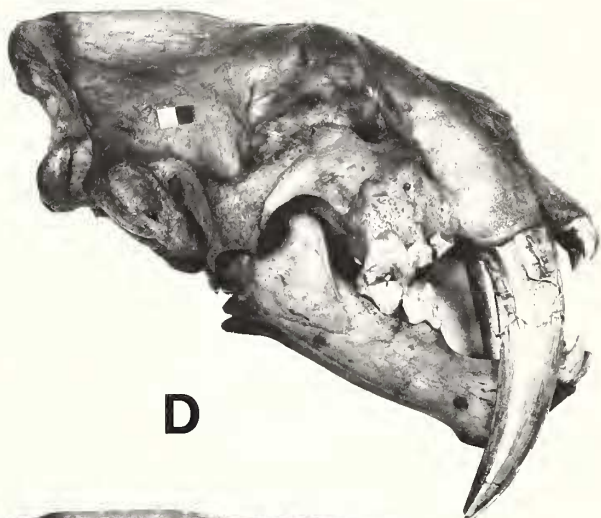
A



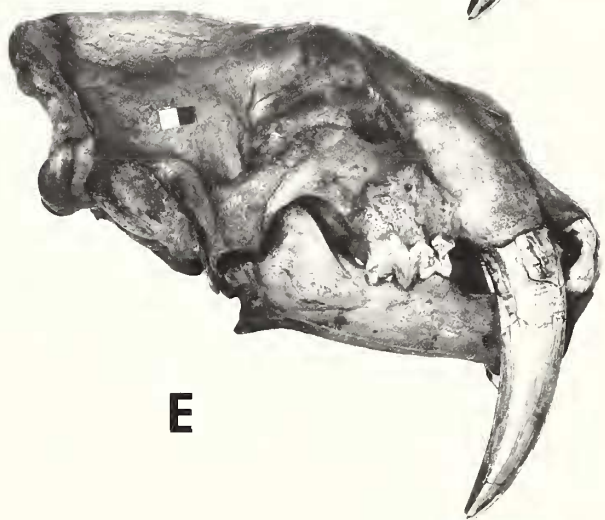
B



C



D



E

teeths, Fabrini (1890) appeared to believe that canine opposition occurred in all and hypothesized a mode of attack in which a bite was used to pierce the body of the prey then the head was pulled posteriad to shear through the mouthful of flesh. He also described an upper canine of *Machairodus nestianus* which bore a facet on its medial surface formed by wear against the lower canine. Matthew (1901), however, denied that canine opposition could have occurred in any sabertooth. Schaub (1925) noted the presence of canine opposition in *Machaerodus crenatidens* but believed that it did not occur in *Machaerodus aphanistis*, *Machaerodus cultridens*, and *Smilodon*. (Taxonomic designations used above are those given by the cited authors and may not reflect currently used synonymies.) Marinelli (1938) specifically stated that *Smilodon* was incapable of biting with the canines. The potential for canine opposition and canine biting in sabertooths appears to have largely disappeared from consideration in subsequent work except for passing mention by Bohlin (1940) and a comment by Kurtén (1963) that the *Smilodontini* evidently used their sabers exclusively in stabbing, whereas the Homotheriini used them in biting as well as stabbing and slashing. The retention of canine opposition in *Smilodon*, in spite of all the other structural modifications, strongly indicates that biting with the canines was very important. If stabbing or slashing were the primary mode of attack, I would expect canine opposition to have been lost and a different relationship, more efficiently adapted for stabbing or slashing, to have evolved. A similar point was made by Bohlin (1940) in that the curvature of the sabers was not suited for a stabbing attack. Can the various adaptations of *Smilodon*, then, be explained in terms of a biting mode of attack?

The arc of lower canine movement centers at the temporomandibular articulation while the center of canine curvature lies several centimeters ventral to this articulation as previously described (Fig. 6). The non-coincidence of these centers results in a constantly changing relationship of the upper and lower canines during closure of the mouth as shown in Figure 7. As the mouth closes beyond the point where the tips of the canines pass, the lower canine moves anterior relative to the upper or it can be stated that the saber progressively moves posteriad relative to the mandible, ultimately all but filling the diastema. As a result, the distance between the tip of the lower canine and the serrate posterior margin of the upper canine progressively increases. In Figure 7B, the shortest distance between the tip of the lower canine and the posterior edge of the upper canine is about 10 mm, in Figure 7C, 30 mm, in Figure 7D, 45 mm, and in Figure 7E, 55 mm. If a piece of flesh were anchored by the tips of the lower canines (and, perhaps, also by the sharp lower incisors and the opposing corrugations of the palate and the sharp diastemal crests of the mandible), closure of the mouth would result in the upper canines shearing through that piece of flesh. I propose the term "canine shear-bite" for this type of bite as opposed to the "canine puncture-bite" used by living mammalian carnivores.

As is readily obvious from the above photographic se-

quence, normal individuals of *Smilodon* could not develop wear facets between the upper and lower canines. However, only a slight developmental error would result in their contact. One left saber, LACMHC 7037, exhibits wear from the lower canine on its medial surface (Fig. 9D). The slightly arcuate facet is longitudinally striated and about 6.5 cm in total length but only the most distal 4 cm is deep enough to expose the dentine.

MECHANICS OF THE CANINE SHEAR-BITE

This mode of attack involves more than simple closure of the mouth with the mandibular musculature. As *Smilodon* pressed its gaping mouth against the body of a prey animal and began to close the mandible, the tips of the opposing canines started to fold the skin and flesh of the prey (Fig. 8A). By the time that the tips of the canines approached each other, they produced a strong fold in the anterior region of the mouth and began to penetrate the "neck" of that fold (Fig. 8B). At about this stage, the poor lever arm of the coronoid process and reduced masseteric musculature resulted in *Smilodon* being unable to close its mouth further by using only the mandibular musculature and the mandible became nearly stationary relative to the body of the prey. It was then anchored by the mandibular musculature and by pressing the well-developed anterior portions of the mandibular flanges against the prey. This pair of laterally flared, narrow ridges would have provided a very good grip when pressed against an animal, more so than if the entire anterior of the mandible protruded anteriorly. Completion of the bite was accomplished by using the head-depressing muscles to drive the cranium against the immobilized mandible with the upper canines shearing through the lateral margins of the fold of flesh (Figs. 8C, D). The serrate distal portion on the anterior margin of the saber facilitated initial penetration while the rounded, non-serrate proximal portion prevented anterior enlargement of the wound at the expense of posterior shear during later stages of the bite. There may have been a sequential use of the head-depressing muscles with the atlantomastoid musculature, best oriented for initial saber penetration, acting first. Those which move the axis of the saber more obliquely would, perhaps, contract in later bite stages. The short lower canines, with probably some assistance from the tips of the lower incisors, could only penetrate deeply enough to anchor the fold. At some intermediate stage, the opposing ridges and grooves of the palate and the diastemal ridges of the mandible gripped and helped to stabilize the fold of flesh. As the head was depressed, the posterior of the mandible would also move ventrad and rotate the anterior so that more of the mandibular flange would contact the prey. This anchored the mandible even more firmly to oppose head depression and resulted in the incisors rotating away from the prey to stretch and thin the neck of the flesh fold. During the final stages of the bite, the upper and lower incisor batteries (which now functionally included the lower canines) punctured the neck of the flesh fold with a closely spaced series of perforations. *Smilodon* could then free the entire

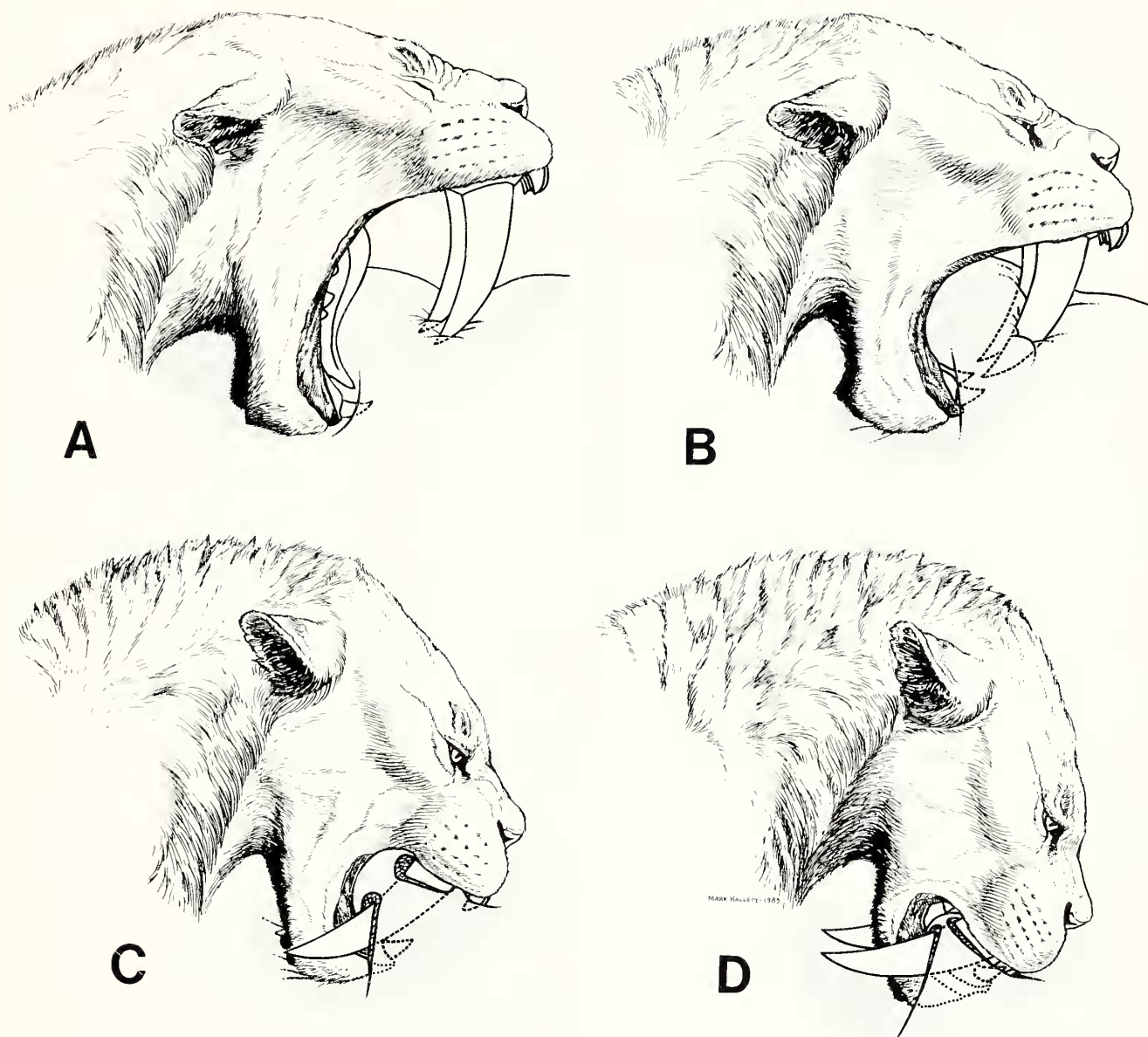


Figure 8. Reconstruction of canine shear-bite sequence in *Smilodon*. See text for explanation. Drawn by Mark Hallett.

fold of flesh with only a modest pull, leaving a major wound in the body of its prey.

SUPPOSED EVIDENCE OF STABBING FROM WOUNDS FOUND IN SKULLS

Three specimens have been described as bearing wounds attributed to stabbing by sabertoothed mammals. Scott and Jepson (1936) described a skull of *Nimravus* with an obliquely directed, elongate, and partially healed wound to the left frontal. They noted that the size and shape of the wound conformed to the upper canine of *Eusmilus* and concluded that this specimen provided evidence that *Eusmilus* stabbed

with its sabers. The size and shape of the injury appear to be consistent with damage inflicted by a saber, but the specimen lacks conclusive evidence—part of a saber within the wound. Even if we assume that a saber caused the damage, it need not have resulted from a stab. A saber puncture could have just as easily, or more easily, been accomplished with a bite. The head of *Nimravus* appears to be small enough to have been taken into the mouth of *Eusmilus* and bitten. This specimen does not provide any solid evidence regarding the mode of attack used by sabertooths.

Miller (1969, 1983) used the above specimen and two others from Rancho La Brea to support a stabbing attack for

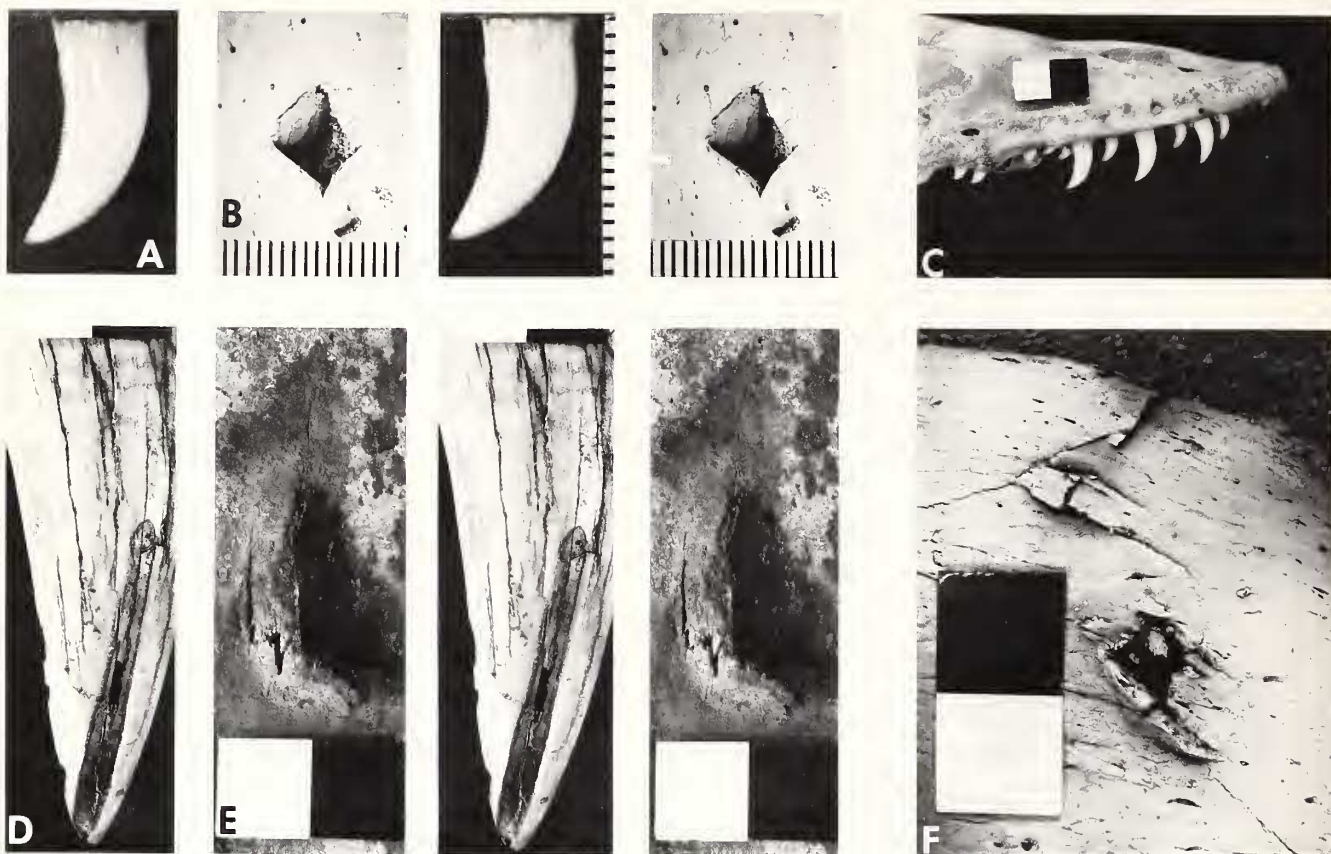


Figure 9. *Varanus komodoensis*, LACM Herpetological Collections 121971. A. Stereopair of upper tooth. C. Upper dentition. Damage to *Smilodon* scapulae inflicted by a square-ended pick about 1915. B. LACMHC K-50, stereopair of pick entry hole. E. LACMHC K-232, stereopair of oblique blow from pick. F. LACMHC K-50, reverse side of different pick hole from that shown in B. Note depressed bone flake, lack of bone flake detachment, and splintery fractures usually typical of damage to fresh bone. D. Stereopair of medial surface of *Smilodon* left upper canine showing wear facet from lower canine. Scales: A and B in mm, others in cm. B and F coated with ammonium chloride.

sabertooths. The only information available for one of the latter specimens is a brief mention by Moodie (1923:128) "A skull of a young wolf the brain case of which is cut through by the tooth of a tiger, the saber being broken off and imbedded in the preserved skull, is on exhibition at the University of California." Since this specimen has never been illustrated or adequately described and cannot presently be located in the Berkeley collections (J.H. Hutchison, pers. comm., 1983), it does not provide useful information about mode of saber use. The other La Brea specimen cited by Miller (1983) is a *Smilodon* skull (LACMHC 2001-24) with an elongate, anteroposteriorly oriented perforation of the left frontal. Relative to the skull orientation, this injury has a rounded posterior margin and a pointed anterior margin, very similar to the cross section of a saber oriented so that the anterior margin of the saber is at the posterior margin of the perforation. An isolated saber, however, can be inserted from either direction. S. Shermis (pers. comm., 1983) conducted a pathology study of this specimen and concluded that characteristics of the injury are compatible with insertion of a saber from the anterior of the individual while the animal

was still alive. In Rancho La Brea specimens, however, damage known to be of recent origin often has characteristics considered to be indicative of injury which occurred during life or soon after death (Figs. 9B, E, F). This probably results from the unusually good preservation of collagen in bones from Rancho La Brea (Ho, 1965; Doberenz and Wyckoff, 1967).

While the conclusive evidence of a broken saber in the wound is again lacking, the evidence does indicate that an upper canine of *Smilodon* could have caused the damage. But is this evidence for stabbing? With a maximum 3-cm clearance between the arcs described by the tip of the canine and the tip of the mandible, the position of the injury does not allow sufficient clearance for either an anterior or posterior attack without the attacker first striking its mandible against the skull. In order to determine if any method of stabbing would be feasible, the injured specimen was manipulated with another skull bearing mandibles mounted at maximum gape. All four attack possibilities were attempted: posterior stab with left saber, posterior stab with right saber, anterior stab with left saber, and anterior stab with right

saber. In both the posterior stab with left saber and the anterior stab with right saber, the opposite saber contacted the skull in the area mediad to the right postorbital process and prevented insertion of the attacking saber. In both posterior attacks, contact of the mandible with the posterior of the injured cranium prevented the attacking saber from striking the skull at the proper angle to produce the observed injury, but a more elongate perforation could have been produced. Both types of frontal attacks had similar results from the mandible striking the anterior of the head. The observed injury could not have been the result of an open-mouthed stab by another *Smilodon*. It could, however, have been the result of a canine blow struck with the mouth closed. An upper canine of *Smilodon* inserted in the injury does penetrate to the depth consistent with the maximum length of exposure ventral to a closed mandible. Therefore, it seems plausible that (if one assumes that a saber was actually responsible for the perforation) the injury may have been caused by an accidental blow struck with the mouth closed during intraspecific combat.

A specimen recently collected by the Rancho La Brea Project deserves mention here. The left third rib of a *Smilodon* (LACMRLP R25876) had the very tip of a *Smilodon* upper canine (separately cataloged as LACMRLP R25877) imbedded in its anterolateral surface. This specimen was found with the left fourth rib of a *Smilodon* in very close to life position but no other elements can be reasonably associated with the two ribs. The puncture produced by the canine appears to have been made in green bone. Its long axis is nearly transverse to the length of the rib with the anterior end (relative to rib orientation) slightly dorsad to the posterior end. The saber tip is obliquely broken; the distance from the tip to the break is between 3 and 6 mm. The margin with the greatest portion remaining appears to be the posterior and occurred in the posterior margin of the puncture. Therefore, the bite was probably made from a posterior and slightly ventrad orientation. Depending on the forelimb orientation of the bitten individual, the saber may have passed through the posterior part of the scapula. None of the *Smilodon* left scapulae from this area of the excavation exhibits possible saber damage but several lack the posterior portion. Other specimens from Rancho La Brea also suggest intraspecific strife (S. Shermis, pers. comm., 1983).

It is interesting that all of the specimens which supposedly show some evidence of damage inflicted by the upper canines of sabertooths are from carnivores. The lack of herbivore specimens displaying saber injury is indirect evidence that bony areas were avoided during predation. Intraspecific or interspecific combat among carnivores is quite different from predatory attack behavior (e.g., Schaller, 1972; Bertram, 1978; Leyhausen, 1979). Therefore, even if the wounds in these specimens were actually caused by sabers during life, they should not be considered as indicative of sabertooth predatory behavior.

SOCIAL STRUCTURE IN *SMILODON*

Hunting techniques employed by various predators are dependent in part upon whether they seek prey in a group with

cooperative behavior or alone (except for a female with young). Although this is almost impossible to interpret for extinct forms which do not have close living relatives, a few inferences can be drawn about social structure in *Smilodon* from the fossil record at Rancho La Brea. As Gonyea (1976) pointed out, the large numbers of *Smilodon* preserved at this locality strongly suggest that they lived in groups or prides.

The LACM made a large collection of fossil vertebrates, now termed the Hancock Collection, from Rancho La Brea between 1913 and 1915. Few of these specimens have been exchanged or lost so that the relative numbers of the larger taxa presently in this collection should be a very close approximation to the preserved thanatocenose. Only about one third of the Hancock Collection, roughly 260,000 specimens, has been cataloged to date. A number of years will be required to complete the task and produce a definitive census of the megafauna, but it is obvious that larger taxa with the lowest proportion of cataloged elements are eoyote and *Smilodon*. Marcus (1960) used the catalogs plus complete counts of *Bison* and *Camelops* in his census of the megafauna and arrived at a total of 1029 as the minimum number of *Smilodon* in the collection. Miller (1968), however, estimated about 2100 individuals of *Smilodon* based on cranial elements.

Unpublished data, briefly reviewed by Akersten, Shaw, and Jefferson (1983), from a recent excavation at Rancho La Brea indicate that entrapment in shallow asphalt seepages was the primary mode of producing the rich fossil deposits at Rancho La Brea. An episode of entrapment apparently began when one large animal (probably an herbivore since these would be most common in natural large mammal populations) blundered into a shallow puddle of asphalt. The helpless or dead herbivore would then attract a number of opportunistic carnivores, thus accounting for the fact that carnivores make up about 90% of the larger mammals found at this locality. The total number of large herbivores should closely approximate the total number of entrapment episodes. Marcus (1960) counted 423 individuals of large herbivores (*Bison*, *Camelops*, *Nothotheriops*, *Glossotherium*, and *Equus*). Allowing for a few proboscideans and uncataloged or lost specimens, the maximum number of individual herbivores and, consequently, the number of entrapment episodes represented in the Hancock Collection is considerably fewer than 600. Therefore, an average of 1.7 to 3.5 *Smilodon* were caught during each entrapment episode, depending on the count used for *Smilodon*. As it is unlikely that all entrapped herbivores lured *Smilodon* in equal numbers, as many as six or eight may have been caught during a single entrapment episode—a period of weeks or several months at the most. This ratio would be improbable if *Smilodon* were a solitary hunter unless, unlike living large predators, a number of individuals shared overlapping hunting areas. The best explanation of these data, providing that the mode of entrapment is correctly interpreted, is that *Smilodon* was a social animal and may have hunted in groups.

Another way of looking at the same data is to compare the relative numbers of *Smilodon* at Rancho La Brea with those of other predators, whose social structure is known or

can reasonably be inferred. The other very common predator is *Canis dirus* Leidy with at least 1646 individuals represented in the Hancock Collection (Marcus, 1960), approximately equal to *Smilodon*. Though *C. dirus* is extinct, its morphology is quite similar to the extant *C. lupus* and a reasonable conclusion would be that it also hunted in fairly large groups. The other common, but smaller, predator is the extinct *C. latrans orcutti* (Merriam), very closely related to the living coyote (Nowak, 1979). Marcus accounted for 239 coyotes in the Hancock Collection but, as previously noted, much of the coyote material has not been cataloged. Coyotes are also social animals but usually form smaller groups than wolves. Carnivores which do not hunt in packs, *Felis concolor*, *Panthera onca* (Jefferson, 1983), *Ursus americanus*, *Ursus arctos*, *Lynx rufus*, *Urocyon cinereoargenteus*, and *Taxidea taxus*, are comparatively rare at Rancho La Brea. Thus, if the relative abundance of carnivores preserved at Rancho La Brea reflects hunting behavior, *Smilodon* must be included among the social forms. As the American lion, *Panthera atrox* (Leidy), is relatively uncommon with 76 individuals reported by Marcus, the same line of reasoning suggests that this predator was either a solitary hunter or, if it hunted cooperatively, groups did not often frequent the area.

Finally, evidence that *Smilodon* may have been a social animal derives from the relatively high frequency of individuals from Rancho La Brea which either could not have killed prey or would have had great difficulty in doing so. Seven adult skulls in the collection had only one saber during life as shown by the undeveloped or secondarily lost alveolus for the other. The remaining canine alveolus in one of these specimens is small and distorted. One or both canines in several skulls were broken off and subsequently worn during life. Individuals lacking one or both canines would probably experience difficulty making a kill. Many postcranial elements of *Smilodon* in the Hancock Collection exhibit pathology, some very severe (Moodie, 1926, 1927, 1930). At least one limb was all but useless in some individuals; vertebral abscesses and fusions would have hampered or crippled many more. A number of skulls also have badly worn cheek teeth (Miller, 1968). Solitary carnivores possessing such major disabilities soon perish unless they manage to survive by scavenging. These same disabilities, however, would place them at an extreme disadvantage when competing with healthy individuals for carrion. Most living large carnivores regularly attempt to appropriate carcasses from other predators. Social carnivore groups, on the other hand, frequently allow incapacitated individuals to feed on kills made by other pack members. Schaller (1972) and Bertram (1978) describe a number of occasions when African lions (especially females) incapacitated by age or injury, survive by feeding on kills made by other pride members. Even aged nomadic males may survive as members of nomadic groups or by being allowed to feed at the kills of other nomads (e.g., Schaller, 1972:81). Schaller (1972:358) even considers that one function of the lion's social system is to provide "life insurance" for individuals unable to hunt for themselves but the selective advantage of this is difficult to envision. Kruuk (1972) noted

that older female members of spotted hyaena clans, no longer able to run well, feed from kills made by other clan members. The African wild dog appears to have the most highly developed social structure among the fissioned carnivores. Estes and Goddard (1967:68) report that the pack provides food for "sick and old adults unable to kill for themselves."

It has been suggested that the frequency of pathologic *Smilodon* specimens from Rancho La Brea was a result of crippled individuals specializing in feeding from the carcasses of trapped animals (Bohlin, 1947). However, if one assumes that the Hancock Collection represents only 10% of the total individuals of all species that were once trapped in these deposits, the 600 episodes of entrapment represented by this collection become 6000, spread over at least 25,000 years or an average of no more than one every four years. Even allowing for a probable clustering of entrapment episodes through time, this could hardly represent a dependable source of food, especially considering the hazards of scavenging at such a place and the necessity of competing with healthy carnivores for carrion.

Although the data regarding *Smilodon*'s social behavior are far from conclusive, they are more easily explained by a cooperative model than by a solitary model. It is not possible, however, to draw inferences about the extent of cooperation during the hunt. They may have merely hunted the same area with each attack made by an individual acting on its own, then fed as a group, or they may have cooperated to a greater degree throughout the hunt.

PREY SPECIES

It has generally been assumed that the sabers of *Smilodon* and other sabertooths were adaptations for attacking large, relatively thick skinned prey such as ground sloths or proboscids. The only direct evidence available comes from the Late Pleistocene fauna of Friesenhahn Cave in Texas (Evans, 1961; Meade, 1961; Lundelius and Slaughter, 1971; Graham, 1976, pers. comm., 1983; Rawn-Schatzinger, 1983). This cave appears to have been a denning site for *Homotherium* to judge from the number of individuals recovered and especially from the occurrence of several very juvenile specimens. Scores of juvenile proboscids, primarily mammoths, were also found but adult proboscids and other large carnivores are rare. This association of an apparent denning site with the remains of juvenile proboscids strongly suggests that *Homotherium* preferentially hunted juvenile proboscids and brought their remains back to its lair. Perhaps the coarsely serrate margins of *Homotherium*'s sabers and other teeth facilitated dismembering the carcasses into more easily carried chunks. The incisors, in particular, are almost shark-like with very serrate margins.

If the herd and parental behavior of extinct proboscids were similar to those of modern African elephants, hunting juveniles could have been a hazardous occupation. Many or all of a herd of elephants will defend or aid any juvenile; they may even continue to defend the body several days after death (Douglas-Hamilton and Douglas-Hamilton, 1975). Even if mammoth behavior were more like that of Indian

elephants with separate nursing and juvenile care units, as suggested by Graham (1976, pers. comm., 1983), attacking predators would have had to be cautious. Whatever the case, *Homotherium* probably waited for an ideal opportunity and retreated immediately after even a successful attack on a juvenile until the adults left the area.

It is certainly tempting to extend this interpretation of *Homotherium*'s prey to *Smilodon* (and other sabertooths), but the two genera have different morphologies (Meade, 1961; Churcher, 1966), even different dental eruption sequences (compare Rawn-Schatzinger, 1983, with Tejada-Flores and Shaw, 1984). In addition, the shear-bite of *Smilodon* would have been equally effective on smaller, thin-skinned prey. The powerful build of *Smilodon* indicates that they probably could have successfully attacked any of the larger herbivores found at Rancho La Brea except for adult proboscidi-ans because they are quite common in many La Brea deposits that totally lack proboscidian remains. I doubt that *Smilodon* fed exclusively on members of any one taxon—no living large predator does—but they may have more commonly hunted juvenile proboscidi-ans than did the other Carnivora found at Rancho La Brea.

AREA OF ATTACK

Most researchers have concluded that the upper canines of sabertooths were too fragile to be used on bony areas of their prey but Gonyea (1976), rebutted by Emerson and Radinsky (1980), thought that a stab at the back of the neck or skull was more likely. Even though the sabers of *Smilodon* are much heavier than a knife, they still have a rather slender cross section in comparison to their length. Because of their length, it seems likely that relatively little lateral force near the tip would cause breakage. If they were used in an attack on a bony area, one saber would probably contact bone before the other, resulting in considerable lateral torque and probable breakage (Bohlin, 1947). Repeated contact with bone would also cause wear on the tips of the canines. Leyhausen (1979:33) notes that even the much stouter conical canines, with thicker enamel, of modern cats readily splinter from normal use.

The curated portion of the Hancock Collection was surveyed for sabers with well-preserved tips and fully formed roots. Of 54 adult sabers, one displayed a minute wear facet on the enamel of the tip, two had wear that barely penetrated to the dentine, and only one had an appreciable wear facet: 2 mm wide by 2.5 mm long. Three others exhibited breakage of the very tip with some subsequent wear; this suggests that the one specimen with a larger wear facet may have also resulted from wear after breakage. All of the sabers with tip wear are isolated specimens exhibiting moderate to extreme wear of the serrations and appear to come from older individuals. This information supports the interpretation that the sabers were not employed in attacks on bony areas. The sabers with broken and worn tips, the occurrence of a saber tip in a *Smilodon* rib, and the skulls with more severely broken sabers showing post-breakage wear do show that mis-

takes were occasionally made. Of the 17 juvenile sabers located, 10 had appreciable wear facets on the tips and one had a minute facet. The larger facets tended to be oblique with more wear toward the lateral margins. Perhaps *Smilodon* kittens were less careful with their sabers than adults.

If the interpretation is correct that the canine shear-bite of *Smilodon* was normally directed toward areas in which bone would not be encountered, only the throat and abdomen are possible targets. The throat has been suggested as the focus for a stabbing or slashing attack because of the shallow carotid artery and jugular vein and because most modern felids typically employ a nape or throat bite (Martin, 1980; Emerson and Radinsky, 1980). It seems to me that a throat bite would have to be delivered with precision in order to sever these blood vessels without encountering the cervical vertebrae or, in short-necked juvenile proboscidi-ans, without striking the posterior of the mandible or the anterior of the humerus. Because the tips of the sabers are well outside the visual area of *Smilodon*, a throat bite would be potentially hazardous to these teeth. Leyhausen (1979) states that the neck bite in living felids results from a taxis oriented toward an indentation (the neck) between a large cylinder (the body) and a smaller one (the head). This taxis does not discriminate between throat and nape orientations; the nape bite used by smaller felids is learned. Larger felids may use either nape or throat bites (other points and methods of attack less commonly), possibly depending on prey size or on the learned behavior of the individual. One interesting variation is the bite to the posterior of the cranium employed by jaguars in killing capybaras (Schaller and Vasconcelos, 1978). A jugular/carotid attack by *Smilodon* would require a much more specific taxis than occurs in modern felids, because the process of learning the exact point to bite by trial-and-error would be far too hazardous to the sabers. I also find it difficult to explain the development of extremely elongate sabers in *Smilodon* and other dirktooths in terms of a throat attack. The shorter sabers of scimitar-tooths should be more than sufficient to sever the major blood vessels.

The elongate sabers of *Smilodon* appear to be adapted for causing massive damage with a single bite. The large, bone-free abdominal region, with a rich supply of blood vessels and a variety of vital organs, would be a more logical area to wield these weapons. Furthermore, unlike the neck, there would be relatively little muscle tissue for the incisors to penetrate at the end of the bite. The type of accuracy needed in order to sever the jugular/carotid blood vessels without striking bone would not be required, simply a taxis directed toward the region anterior to the hind legs. Most authorities agree that, while large, living felids rarely attack the abdomen, they do typically begin feeding there (e.g., Leyhausen, 1979; Schaller, 1972). African lions, after pulling down large prey such as rhinoceros and hippopotamus, are known to occasionally attack the abdomen instead of the throat (J. Kingdon, pers. comm., 1983). Wolves (Young, 1944; Mech, 1970), African wild dogs, golden jackals (van Lawick-Goodall and van Lawick-Goodall, 1971), and spotted hyaenas (Kruuk, 1972) frequently kill by attacking the abdomen. This is probably the only vulnerable area easily available to such

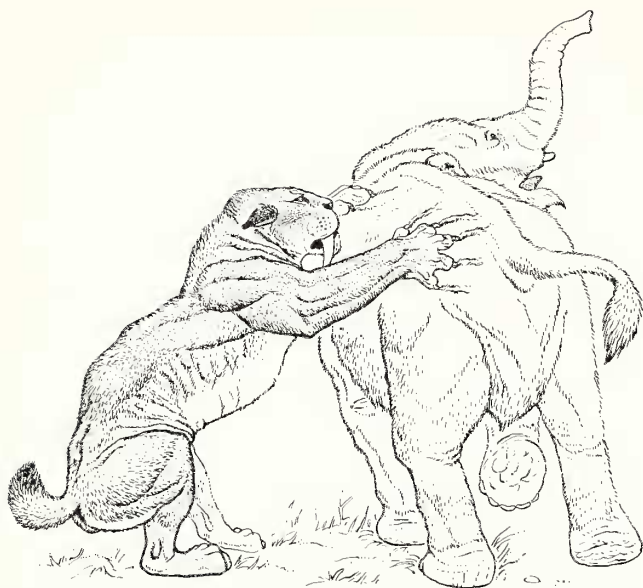


Figure 10. Reconstruction of initial stages of attack by *Smilodon*. Left, pulling down young mammoth. Right, beginning of canine shear-bite to abdomen. Drawn by Mark Hallett.

packs of relatively small predators which lack the claws and bulk to pull down their prey in order to attack other vital areas. Even so, it does show that abdominal attack can be effectively used by modern mammalian carnivores.

Martin (1980) considered an abdominal attack by saber-toothed cats, especially by dirktoothed forms such as *Smilodon*, to be very improbable. He argued that the prey would not be killed immediately and, unless it went into total shock, would try to escape from the attacker which was not adapted to pursue an escaping animal. He also claimed that the abdomen can be defended by the head of the prey and that stabbing a broad, gently sloping abdominal area would be difficult at best. I concur with the last point; however, the canine shear-bite is perfectly adapted for attacking such areas. Furthermore, it is difficult to visualize how the forms which were potential prey for *Smilodon* at Rancho La Brea could have used their heads to defend their abdomens while stretched out on the ground. Figure 10 depicts *Smilodon* pulling down a juvenile mammoth and initiating a canine shear-bite to its abdomen.

In regard to the prey attempting to escape, Schaller (1972: 266) stated that prey pulled down by lions and not yet bitten appeared to go into shock and rarely struggled to any extent. He went on to describe an uninjured buffalo that lay on its side while its tail was chewed by a lioness. Auffenberg (1981) credited shock as being important in the lack of struggle evinced by downed but not yet killed prey of *Varanus komodoensis*. Furthermore, tigers are easily able to control large, struggling prey after bringing them down (Schaller, 1967). I doubt that prey would make much of an attempt to escape after the shock of being pulled down by *Smilodon* and having a huge chunk of the abdominal region torn out. The claws

and powerful forelimbs of *Smilodon* would easily be able to control any who might try to struggle. Even if an occasional prey animal could escape after the attack, its severe injuries would prevent it from running very fast or very far.

A POSSIBLE KILL SCENARIO

Events in a typical attack sequence might have taken the following course, assuming that *Smilodon* did cooperate to a minor extent during the hunt, that the prey in this particular case was a juvenile mammoth, and that mammoth social behavior was similar to that of modern Indian elephants (Graham, 1976, pers. comm., 1983).

A pride of sabertooths scatter out while approaching a herd of adult female and juvenile mammoths, targeting one pair of juveniles who were playing a short distance from the rest. While several of the predators distract the herd, one makes a short rush from concealment and pulls one juvenile down toward itself with the retractile claws and powerful forelimbs. Quickly orienting itself to the posterior of the abdomen, the sabertooth opens a gaping wound with a canine shear-bite, then flees before the mother and the rest of the herd can retaliate. The pride regroups at a distance and waits for the critically injured juvenile to die and for the rest of the herd to leave. Once the dead animal is abandoned, the sabertooths (including aged or incapacitated members of the pride) return to feed. They tear the carcass apart with their prognathous incisors and occasionally employ a canine shear-bite to open up a new area. The rather long lips of sabertooths allow them to take chunks and strips of flesh into the side of the mouth so that the highly developed carnassials can slice the meat

into pieces small enough to swallow (Miller, 1969; Martin, 1980).

A MODERN ANALOG, THE KOMODO DRAGON

A major problem in interpreting the mode of attack in sabertooths has always been the lack of a modern analog. No living mammalian predator has teeth comparable to the sabertooth canine and none is known to consistently kill its prey by first pulling it down then biting open the abdomen, as I hypothesize for *Smilodon*. If one looks at non-mammalian predators, however, one very interesting modern reptilian analog stands out: the Komodo dragon (*Varanus komodoensis*). Auffenberg (1978, 1981) has thoroughly studied this large active predator, which may grow up to 3 m long and 60 kg in weight. Its dentition consists of mediolaterally flattened, sharp, recurved teeth with serrations on the entire posterior margins and about the distal one fourth of the anterior margins. Although this reptile has numerous teeth in both upper and lower dentitions, the individual teeth quite closely resemble the canines of *Smilodon*, even in the distribution of serrations (Figs. 9A, C).

The usual prey of the Komodo dragon consists of deer and boar. Recorded kills include deer of up to 80 kg and boar up to 40 kg, but villagers report kills of deer up to 200 kg. The Komodo dragon typically kills these prey by ambush along game trails or in bedding areas. Because it lacks prehensile forelimbs, it grasps them with the mouth, pulls or wrestles them down, then bites open the abdomen. Small individuals may be picked up in the powerful jaws and shaken. Attacks on tethered goats indicate that they appear to be in shock prior to their abdomens being ripped open; death probably results from "massive visceral bleeding" (Auffenberg, 1981: 247). As Auffenberg further notes, visceral bleeding could be enhanced by physiological shock resulting from the violent attack.

Successful attacks on larger prey, such as tethered or free water buffalo up to 590 kg, apparently follow a different initial pattern. The Komodo dragon lacks the strength to bring down such large prey but a few individuals learn to repeatedly bite and slash at the legs until the animal is crippled by the severing of its tendons and collapses. Available indirect evidence indicates that the kill is again accomplished by biting open the abdomen (Auffenberg, 1981:261). Unlike *Smilodon*, the Komodo dragon can afford to attack bony areas such as lower legs because it has numerous and replaceable teeth; however, it still makes the killing bite to the soft abdomen after bringing the animal down. That it can easily bite open the abdomen of a large water buffalo with saber-like teeth only 2 cm or less in height surely shows that the sabers of *Smilodon* could very effectively function in a similar manner. The method of biting also differs in that the Komodo dragon delivers repeated bites with backward jerks at the same spot. Despite the number of differences, I suggest that this reptile is the closest living analog to *Smilodon* in kill methodology.

Other indirect evidence tends to support the analogy. The prey animals of the extant Komodo dragons appear to have been introduced by man. Pleistocene deposits on the island

of Flores (within the present range of the Komodo dragon) appear to contain only two large animals, both miniature stegodont elephants (Hooijer, 1972a). On Timor, east of the Komodo dragon's present range, Pleistocene deposits have yielded large varanid vertebrae similar to *Varanus komodoensis* in association with the same proboscidiens and giant tortoises (Hooijer, 1972b). Large varanid vertebrae are also known from the Pleistocene of Java (Hooijer, 1972b) with a more varied fauna including proboscidiens. These data led Auffenberg (1981:289) to suggest that the ancestors of Komodo dragons once fed on small proboscidiens. Thus, a tentative parallel can be drawn between the prey of Pleistocene Komodo dragons and, at least, *Homotherium*.

In addition, Australia stands out as the only temperate continent which lacks the remains of some type of saber-toothed mammal. This seems odd because the carnivorous marsupials there underwent as extensive a radiation as did the South American marsupials which did evolve a saber-toothed form. Varanids are, however, known in Australian faunas by the Middle or Late Miocene and underwent a major radiation, culminating in the giant, Late Pleistocene *Megalia prisca* Owen which reached a total length of perhaps 7 m and a maximum weight of 600 to 620 kg (Hecht, 1975). The teeth of *Megalia* closely resemble (but are larger than) those of *Varanus komodoensis*, suggesting a similar, highly predaceous mode of life. Hecht believed that *Megalia* was the major predator of the Late Pleistocene giant marsupials of Australia. Perhaps *Megalia* and other large fossil Australian varanids occupied a niche similar enough to saber-toothed mammals that they precluded marsupial carnivores from that adaptive zone.

CONCLUSIONS

The hypothesis that *Smilodon* pulled down its prey, then killed with a canine shear-bite to the abdomen, appears to be consistent with all of the observed morphology relevant to use of the upper canines and eliminates several anomalies introduced by stabbing or slashing hypotheses. The powerful head-depressing muscles function to bite by means of depressing the cranium against an essentially stationary mandible, held in place by pressing the anterior margins of the mandibular flanges against the prey. The mandible needs to be very robust to resist the developed forces but does not require a long coronoid process in order to bite with the canines. The lower canines are relatively small because they need only penetrate enough to anchor the fold of flesh taken into the mouth until the very end of the bite, then they function with the incisor battery. In the shear-bite model, a tremendous force is no longer needed to drive the sabers into the prey. The geometric relationships of the cranium, mandible, and dentition are far easier to explain. The palatal ridges and grooves serve as gripping devices in the absence of most of the premolars. One could even speculate that the retracted nose of *Smilodon* (Miller, 1969) was an adaptation to avoid friction burns from rubbing against the hair of its prey during the head depressing stages of the canine shear-bite. The problem of structural and behavioral intermediates

between biting and stabbing/slashing forms disappears. The similarities between the kill behavior hypothesized here for *Smilodon* and that observed in the living *Varanus komodoensis*, plus the correspondence in dental morphologies between the two, add the dimension of a modern analog.

Examination of fairly complete and undistorted specimens, casts, and figures of other sabertoothed mammals indicates that they all very probably possessed upper and lower canine occlusion similar to that of *Smilodon*. Therefore, I believe that the canine shear-bite was utilized by all, even though the details of its use must have differed as demonstrated by the variety of other morphologic features exhibited by various taxa. The shorter sabers of *Homotherium* may have been more useful in a throat attack and the coarser nature of their serrations may indicate that these teeth were more frequently employed for some purpose (such as to dismember carcasses) in addition to the kill. In *Thylacosmilus*, the lack of upper incisors, the ever-growing upper canines, the blunt lower canines which honed the uppers, and the longer series of cheek teeth (Riggs, 1934; Turnbull, 1978) clearly show that the canine shear-bite of this genus must have differed in many details. The morphological differences between other sabertooths and *Smilodon* are many, but I believe that they do not negate the hypothesis that all employed some variation of the canine shear-bite to kill prey.

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